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A SYSTEMATIC STUDY OF THE FAMILY POLYORCHIDAE (HYDROMEDUSAE)*

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Acknowledgment

I wish to express my appreciation to Professor S. F. Light and Dr. R. Stohler of the University of California, Berkeley, for their courtesy in procuring and sending me material of *Polyorchis penicillatus* from San Francisco Bay, California, one of the localities from which A. Agassiz obtained his specimens and possibly one of the sources of Eschscholtz' type material; and to Professors J. E. Lynch and T. Kincaid for sending me material of this genus from the Puget Sound region, Washington.

General Classification

The classification of the Hydromedusae offers very serious difficulties, a fact recognized even by some of the early investigators, e.g., Gegenbaur (1856, p. 217). Indeed, even the segregation of two of the main subdivisions of this group, viz., the Anthomedusae and the Leptomedusae, is both difficult and confusing. For this reason it was a most gratifying development when, mainly through the efforts of R. Weill, the study of the nematocysts opened up a new and very promising approach to this problem. In his large, monographic summary, Weill (1934) demonstrated clearly that, if one takes into account all the different types of nematocysts occurring in a species, i.e., the cnidome, one usually obtains a clear-cut indication as to the true position of this form in the natural system. The new method, unfortunately, has some quite serious

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limitations: fresh material is often indispensable; the nematocysts frequently are extremely small and, in addition, are refractory to stains.

To the medusae of uncertain systematic position, between the Anthomedusae and the Leptomedusae, belongs one of the most commonly seen forms of the coastal waters of western North America—*Polyorchis penicillatus* (Eschscholtz). A brief account of the systematics of this species and of those which have been taxonomically more or less closely associated with it will give a convincing illustration of the confusion which has pervaded the field and at the same time will demonstrate what difficulties may be resolved through the application of facts brought out by a careful analysis of the cnidome.

Polyorchis penicillatus was established by Eschscholtz in 1829 under the name of *Melicertum penicillatum*. The genus *Melicertum* was very ill-defined and was placed, with six other genera, under the family Oceanidae, a unit which, as conceived by Eschscholtz, was extremely heterogeneous indeed. In brief, the first systematic allocation of this form was uncertain and may be said to have resulted from a guess, quite in accordance with the primitive state of the scientific knowledge of the Coelenterata in those early days of zoological investigation.

The same may be said about the decision made by de Blainville (1834) to remove this form to the Trachymedusan genus *Aglaura* Péron and Lesueur. This unfortunate choice evidently was caused by the fact that *Aglaura hemistoma* Péron and Lesueur has a deep bell-like shape and pendent, sausage-shaped gonads.

The first to submit *P. penicillatus* to careful examination was A. Agassiz whose results appeared in a preliminary form in L. Agassiz (1862, pp. 349, 352). In this work it was made the type of a new genus, *Polyorchis,* which in its turn was made the sole representative and hence the type of a new family, Polyorchidae, placed in the suborder Sertulariae. This suborder corresponded largely to what we now term the Leptomedusae. (L. Agassiz, 1862, p. 348, although doubtfully, also placed in this suborder forms which we now refer to the Trachymedusae.) In his attempt to establish families within the Leptomedusae, Agassiz met with considerable difficulties because of the incompleteness of the available data. Hence he decided to proceed in accordance with the principle of progressive elimination (p. 352): he distinguished "as belonging to distinct families all those free Medusae and Hydroids which have distinct patterns." Thus *Polyorchis* was made to represent a special family because its members are "quite remarkable for their branching, chymiferous tubes, and their pendent, reproductive organs."

In A. Agassiz (1865), too, Polyorchidae contained but a single genus. This, however, was due to the limitation of the material on which his report was based, as will be seen from the fact (p. 118) that Agassiz actually suggested that the genus *Olindias* F. Müller, 1861 (now belonging to the Trachymedusae) would form a "very natural family" with *Polyorchis,* a suggestion evidently based on the identification of the lobe-like gonads on the radial canals in *Olindias* with the sterile side branches of these canals in *Polyorchis.*

In his monumental monograph, "Das System der Medusen," Haeckel (1879, p. 140) described and analyzed the large family Cannotidae, previously (1877) established by him in a preliminary manner. Haeckel, of course, fully recognized that the 15 genera referred by him to this family are very heterogeneous; indeed, some of the previously described ones had been classified as Anthomedusae while others had been arranged with the Leptomedusae—and some of the latter showed quite divergent features. Haeckel maintained, however, that a careful analysis had convinced him that all of these genera were "echte Leptomedusen" and that they should be placed next to the Thaumantiadae, i.e., near the bottom of the Leptomedusan system. Two of the most outstanding characters of the Cannotidae are the branching of the radial canals and the multiple gonads originating from these canals. The Cannotidae was divided by Haeckel into three subfamilies, one of which was Polyorchidae. This subfamily, however, did not correspond to Agassiz's family of this name, but was a greatly broadened concept. It included, besides *Polyorchis,* the highly diversified genera, *Staurodiscus, Staurophora, Ptychogena,* and *Gonyonema.*

Quite naturally, a systematic unit as diversified as the Cannotidae aroused criticism among later investigators. Among the most important of these critics should be noted Browne (1896) and especially Maas (1904). The former demonstrated that the genus *Willsia* (*Proboscidactyla*), strikingly characterized by its branching radial canals, is not a Leptomedusa but an Anthomedusa since its sex products do not originate on the radial canals but on the manubrium. Maas submitted the whole family Cannotidae to a searching analysis, the result of which was the complete dissolution of this family and the scattering of its component genera to various places in the system. Some of the component members, e.g., the *Willsiidae sens. rect.,* Browne (1896), were allocated to the Anthomedusae, while others, such as the greatly restricted Polyorchidae, were classified with the Leptomedusae. This re-evaluation by Maas (1904) was in a large measure accepted by Mayer in his "Medusae of the World" (1910), a work which forms the main foundation of our modern knowledge of these organisms. Mayer presents the Polyorchinae as a subfamily of the comprehensive family Thaumantiidae, the first of the three large families forming the Leptomedusae.

Throughout these classificatory studies we find emphasis on the branching of the radial canals. However, the fundamental value attributed to this character by Haeckel (1879) was decidedly weakened when Browne (1896) was forced to place some forms with branched canals among the Anthomedusae while others were allowed to retain the position among the Leptomedusae assigned to them by Haeckel. This type of arrangement, of course, implied the tacit admission that branching had occurred more than once in the course of the evolution of the Hydromedusae. In this connection it is of interest to note that quite a long time before Haeckel's large monograph was published, Gegenbaur (1856, p. 219), with his keen sense for systematics, clearly realized that the branching of the radial canals is not such an important character as it may at first appear to be (see below, p. 122).

The first investigator to question the correctness of the allocation of the Polyorchidae to the Leptomedusae was Fewkes (1889*b*, p. 106). In a footnote he wrote as follows: "It is probable that when the *Polyorchis* buds from its hydroid it has four radial tubes, four tentacles and possibly the stumps of four similar interradial appendages. As the radial tubes at that time lack lateral branches, we have in this stage a medusa closely resembling the young *Sarsia*. If my suppositions are correct, there seems no doubt that *Polyorchis* belongs to the true Anthomedusae, and that it is allied to *Sarsia*." This was a bold suggestion, completely at variance with the prevailing ideas of the time. Fewkes's assumption about the number of tenacles was borne out by Foerster (1923, p. 34) who established that the young medusae of *Polyorchis* found in British Columbia have four tentacles until they reach a bell height of approximately 5 mm.

The only one who, up to the present time, has accepted Fewkes's view that the Polyorchidae are true Anthomedusae is Uchida (1927, p. 170) who based this conclusion to a large extent on his examination of the development of *Spirocodon saltatrix* (Tilesius). He found that the youngest recorded specimen of this species "is very similar to *Sarsia* which is the most primitive of the Anthomedusae." In his reconstruction of the evolutionary differentiation of the Anthomedusae, Uchida (1927, p. 168, Fig. 22) placed the Polyorchidae and the Spirocodonidae near the top of the system, next to the Willsiidae; and he judged them to have evolved from the primitive Codoniidae, of which *Sarsia* is a member, and to have passed through an intermediate Tiaridae stage.

It may be worthy of notice in this connection that A. Agassiz stated on p. 132 of his in some respects quite remarkable "North American Acalephae," 1865, that the medusae of *Melicertum* "hold an intermediate position between the Campanularians and the Tubularians, being more closely allied to the latter in their embryonic condition, and assuming as adult Medusae somewhat the aspect of Campanularian Medusae." Since the genus *Melicertum* belongs to the subfamily Melicertinae of the Thaumantiidae, next to the Polyorchinae in Mayer's (1910) large monograph, it is evident that Agassiz to some degree anticipated Fewkes's and Uchida's solution of the problem of the systematic position of the Polyorchidae. Agassiz's figure 203 of the youngest stage of *Melicertum* certainly does show a remarkable similarity to the young medusae of *Polyorchis*.

To summarize: there are at present two fundamentally opposed interpretations in regard to the systematic position of the Polyorchids: (1) the great majority of the investigators consider these forms to be Leptomedusae, located near the base of this group; (2) according to Fewkes and Uchida, they are true Anthomedusae to be placed, with the Willsiidae, at the top of this group, and derived from Codoniidae-like ancestors. Uchida, in addition, believes that they have passed through a Tiaridae-like stage.

Which of these two interpretations is the more correct, according to evidence derivable from the cnidome? The answer to this is quite clear: the Polyorchids are unquestionably Anthomedusae. They are equipped with two types of nettle cells (bicnidome): desmonemes and stenoteles. According to Weill (1934, p. 478), neither of these categories ever occurs among the Calyptoblasts (Leptomedusae) while they are common, though by no means always present, among the Gymnoblasts (Anthomedusae); see Weill (1934, p. 444). Among the Anthomedusae, according to the same source, there is only one genus known to have a bicnidome consisting of desmonemes and stenoteles, and that is the genus *Sarsia*. Hence the close relationship between the Polyorchids and this genus may be considered to be settled with nearly complete certainty. The similarity even extends to quite detailed features of structure, and the peculiarity emphasized by Russell (1938, p. 150), that *Sarsia eximia* is characterized by the fact that its stenoteles occur in two different size classes, is repeated among the Polyorchids. Concerning Uchida's final assumption that the Polyorchids passed through a Tiarida-like stage, the evidence from the cnidome is equally decisive, even though it is derived from only a single member of the family Tiaridae—*Leuckartiara octona* (Fleming). In this form, there are neither desmonemes nor stenoteles, thus conclusively eliminating it and its closest relations from the pedigree of the Polyorchids. In regard to the placing of the Polyorchidae next to the Willsiidae (either among the Leptomedusae or among the Anthomedusae), it may be noted that in *Willsia stellata* Forbes we find (Russell, 1938, p. 154) a cnidome which does not indicate any close relationship. (Note: Uchida, 1927, p. 169, specifically states that he does not know the relationships of the family Willsiidae.)

A further tracing of the ancestry and systematic position of the Polyorchidae is impossible at present because of our fragmentary knowledge of the cnidomes of the various Hydromedusan genera. Suffice it to state that no forms are known, besides *Sarsia* and the Polyorchidae, in which there is a bicnidome consisting of stenoteles and desmonemes.

The preceding discussion may give the impression that the cnidome yields taxonomic clues both simple to establish and incontrovertible in their application. Unfortunately, this a far from being true, although indeed, the *Sarsia-Polyorchis* relationship evidently is one of the simplest examples in this field. Concerning the difficulties inherent in the establishment of the nature of the cnidome, reference is made to Weill (1934) and Russell (1938). These difficulties can be overcome only by very careful work. The really serious obstacles are encountered when we attempt to apply the evidence derived from the cnidome to taxonomic problems. This is due to the fact that the nematocysts, despite their structural complexities, evidently present amazing examples of the mysterious phenomenon which we call convergent evolution. A thorough morphological study of the cnidomes of a large number of genera distributed throughout the entire Coelenterate phylum and analyzed statistically should result in very valuable evidence bearing on the fundamental, although altogether too little understood, problem of convergence.

In his remarkable monograph, the "Medusae of the World," Mayer (1910) classified the orders of the Hydromedusae into families which often in their turn were divided into subfamilies which, in some cases, had their genera arranged into tribes. This classification may have been somewhat too elaborate and graduated considering the immense difficulties inherent in the appraisal of comparative degrees of relationship. Hence it was natural that the criticism of this classificatory system became quite strong and that pronounced changes were proposed. In regard to these changes, Foerster (1923, p. 224) states that the chief difference between the system of Mayer and those of later investigators "lies in the complete abandonment of all sub-families [and tribes]. These have been either elevated to separate families or incorporated in the family without further division." This policy, even though it was to a certain extent justifiable, probably was carried too far. After all, a classificatory system should mirror degrees of relationships to the greatest possible extent. In the present report I have proposed a couple of changes in the most recent classification along this line: the families Polyorchidae and Spirocodonidae have been joined as subfamilies of Polyorchidae *s.l.;* and, in addition, two genera were united and placed as subgenera, *Polyorchis* and *Scrippsia,* under the genus *Polyorchis s.l.* The material in these cases was such that it practically forced me to adopt this solution. It should be noted that the first to suggest the establishment of the Polyorchids and the Spirocodonids as subfamilies was Goette (1886, p. 832).

Family **Polyorchidae** A. Agassiz, 1862

Agassiz, A., in Agassiz, L. (1862), pp. 349, 352;—Agassiz, A. (1865), p. 118;— Haeckel (1879), *part.*, pp. 140, 142, 145, 149;—Goette (1886), p. 832;—Murbach and Shearer (1903), *part.*, pp. 174, 187;—Maas (1904), pp. 421, 423, 441;—Torrey (1909), p. 14;—Foerster (1923), p. 250;—Uchida (1927), pp. 169, 170, 171, 173, 226.

Diagnosis: Anthomedusae of medium to large sizes (height of bell, from about 20 to somewhat more than 100 mm.). Umbrellar outline deeply bell-shaped in lateral view; at least as high as wide. Mesoglea moderately thick to rather thin, except aborally where it forms a more or less pronounced peduncle, the gastric peduncle, from which the manubrium depends. Manubrium quadrate in section. Oral lips 4, simple in young specimens, becoming flaring, recurved, and moderately frilled with age; their edges somewhat thickened with densely set nematocysts forming distinct marginal band, but without oral tentacles. Marginal tentacles increase in number with age, at first probably always 4; in adults numerous, more than 20; simple and hollow, their canals connected with ring canal; armed with numerous, button-like aggregations of nematocysts scattered irregularly over the entire tentacle; when tentacle is contracted, buttons are closely set, except near tentacular base where they become increasingly scarce. Tentacles of different sizes, according to position in sequence of tentacular development; when relaxed, the longest are longer than bell is high. Stomach tubular, without marked enlargement at place where radial canals join it. Radial canals 4; their distal two-thirds sometimes simple, but show pronounced tendency to develop blind side branches on either side of each canal. Gonads located on parts of the 4 radial canals which are on gastric peduncle. Cnidome: bicnidome, consisting of stenoteles and desmonemes. Ocelli present at bases of tentacles. Statocysts and cordyli absent. Appears to be restricted to the Pacific Ocean.*

Remarks: As mentioned on page 106, Goette (1886, p. 832) segregated the Polyorchids and the Spirocodonids as subfamilies. On the other hand, in his excellent study on the Anthomedusae of Japan, Uchida (1927) decided that these forms should be regarded as representing two distinct families. His Spirocodonidae included only *Spirocodon*, while, in the Polyorchidae, Uchida placed two genera, *Polyorchis* and *Scrippsia*. Should the latter arrangement be accepted? A careful inspection of these forms will bring forth three basic facts: (1) Morphologically, these genera are very closely related. (2) This relationship is much closer than the relationship between any one of the three genera and any other genus of the Anthomedusae, a conclusion borne out by the fact that for a long time *Polyorchis* was considered a member of the Leptomedusae rather than of the Anthomedusae. (3) Of the three genera, *Polyorchis* and *Scrippsia* are mutually much more similar than either of them is to *Spirocodon*. These basic facts indicated first, that *Spirocodon, Polyorchis,* and *Scrippsia* should be kept together and, at the same time, be removed from the remaining members of the Anthomedusae; second, that *Spirocodon* should be removed from *Polyorchis* and *Scrippsia*. To accomplish this, it seems most advisable to revert to the classification proposed by Goette, i.e., to maintain Polyorchidae *s.l.* to include all these genera and to divide it in two subfamilies: Polyorchinae, for *Polyorchis* and *Scrippsia;* and Spirocodoninae, for *Spirocodon*. The most fundamental difference between these subfamilies is found in the structure of the gonads.

Subfamily **Polyorchinae**

Gonads in the form of narrow, sausage-like, multiple sacs, freely suspended in subumbrellar cavity.

Remarks: As will be seen from the remarks above, this subfamily includes two previously accepted genera, *Polyorchis* and *Scrippsia*. Since a close examination shows that these units are rather similar, the question presents itself: should these units maintain their present status?

At the time when the genus *Scrippsia* was established by Torrey (1909) to receive a single species, *S. pacifica,* there could hardly have been any rea-

* The statement by Murbach and Shearer (1903, p. 177) that the genus *Polyorchis* has been found in the Adriatic Sea is erroneous.

sonable doubt as to the justification of its establishment. Besides a number of quantitative differences from the related genus *Polyorchis,* the new form exhibited a qualitative differentiating feature: its canal system was simple, that is, it lacked every trace of branching, and branching was considered a characteristic of fundamental importance in *Polyorchis*. The discovery of *Polyorchis haplus* has completely changed the situation. *P. haplus* is a typical *Polyorchis* except in the fact that, until the very latest stages, thus long after the attainment of sex maturity, its canals remain simple. Only in the very largest specimens do the radial canals exhibit a knobby appearance, thus showing that in this species too there is, although nearly concealed, a branching tendency. By this discovery the only qualitative difference between the two genera has been removed. Among the quantitative differences, perhaps the most striking is the decided displacement of the outer tenacles in *Scrippsia* from the bell margin, along the exumbrellar side. However, this difference, too, loses much of its significance when we consider the fact that in the little-known *Polyorchis campanulata* (Chamisso and Eysenhardt), which evidently is furnished with branched radial canals, the oldest tentacles appear to be about as far removed from the bell margin as in *Scrippsia*. The elimination of generic value from these two characters makes, I think, the generic status of *Scrippsia* untenable. However, considering the rather striking difference in general appearance between *Scrippsia* and the typical *Polyorchis,* it may be advisable, at least for the time being, to maintain *Scrippsia* as a systematic unit, assigning to it a subgeneric status. Further knowledge of *Polyorchis campanulata* may make even this status untenable.

Polyorchis A. Agassiz, 1862

Polyorchis: Agassiz, A., *in* Agassiz, L. (1862), pp. 348, 349;—Agassiz, A. (1865), p. 119;—Haeckel (1879), pp. 140, 141, 142, 144, 149;—Murbach and Shearer (1903), p. 174;—Maas (1904), pp. 425, 426, 442;—Loeb (1906*a*), pp. 87, 88, 89, 90, 91, 141;—Hargitt (1908), p. 317;—Mayer (1908), p. 126; (1910), pp. 197, 218;—Torrey (1909), pp. 14, 16;—Little (1914), p. 307;—Foerster (1923), p. 250;—Uchida (1927), pp. 170–173, 227.

Medusa: Chamisso and Eysenhardt (1821), *part.*, p. 359.

Melicertum: Eschscholtz (1829), *part.*, p. 105.

Melicerta: Blainville (1834), *part.*, p. 284.

Aglaura: Blainville (1834), *part.*, p. 283.

Campanella: Lesson (1843), p. 281.

Polyorchidium: Haeckel (1877), no. 148; (1879), p. 150.

Diagnosis: Bell margin straight, i.e., not divided into lobes. Gastric peduncle subconical or rounded. Tentacles throughout life fairly uniformly distributed along entire bell margin. Following appearance of first 8 tentacles (first 4 perradial and then 4 interradial), tenacles increase by multiples of 2, i.e., 2 tentacles appear about simultaneously in each quadrant, resulting in a tentacular series of: (4–8)—16—24—32, etc.* First 24 tentacles originate in a nearly completely fixed sequence (Fig. 1), viz., first, 4 perradial; second, 4 interradial; third, 8 adradial; fourth, 8 between second and third.† Tentacles connected with ring canal by canals of different lengths, due to continued growth of these canals throughout life, canals of earliest tentacles being of moderate length, those of the later tentacles being progressively shorter, the youngest being for all practical purpose absent. Thus tentacles are arranged in concentric, slightly irregular rings, the outermost ones tending to become removed from the bell margin.

Remarks: Since the nomenclatorial correctness of *Polyorchis* has been criticized, and since this question has not yet been properly settled, it may be advisable to submit it to a brief review.

Fig. 1.—*Polyorchis montereyensis*. Diagram showing sequence of formation of tentacles, within one quadrant.

* There is nearly always a slight difference in the time of appearance between members of each pair; and thus it would perhaps be more correct to state that 4 tentacles are added at a time, 1 in each quadrant. However, even though this is true, the difference in size between the members of the pairs soon disappears, and hence it may be permissible and preferable always to deal with these structures as paired.

† Following the fourth group of tenacles, deviations from the "normal" sequence, as expressed in Figure 1, may be found, as shown by the following exceptions found in *Polyorchis montereyensis:* (1) Rate of development not always identical in all four quadrants; e.g., a pair of tentacles found in one quadrant or in two or three quadrants may be absent from the remaining; such an absence of even three tentacles has been observed by me. (2) Sequence of origin may be quite irregular in one to three quadrants and perfectly normal in the rest. (3) Sometimes the bud of a tentacle originates in its normal position but, for some unknown cause, its further development is inhibited.

In his discussion of the genus *Melicertum,* Haeckel (1879, p. 136) states that, if he followed the usual procedure of nomenclature, he would be justified in changing the names of *Melicertum* and *Polyorchis* as used by L. and A. Agassiz (1862) : "so wäre ich vollkommen im Rechte, wenn ich ihre Genera *Melicertum* und *Polyorchis* einfach striche, ihre *Polyorchis* als *Melicertum* und ihr *Melicertum* mit einem neuen Namen bezeichnete; ebenso auch ihre Familie Polyorchidae als Melicertidae und ihre Melicertidae unter neuem Namen aufführte." The only reason why Haeckel did not carry through this radical nomenclatorial change was that Agassiz was the first to give a good description of the genus *Melicertum!* Disregarding this invalid reason, would it be correct to change the name of *Polyorchis* to *Melicertum?* What are the facts in the case?

The first to use *Melicertum* as a generic name was Eschscholtz (1829, p. 105) who introduced it as an emended form of Oken's (1815) *Melicerta.* According to Article 36 of the "International Rules of Zoological Nomenclature," even though generic names differ only in trivial details, e.g., in termination, they should not be regarded as identical: hence the two mentioned names must be dealt with separately. *Melicerta,* as used by Oken, must be discarded as a homonym, yielding to *Melicerta* Schrank (1803), referring to Rotifers. *Melicertum* Oken, now commonly in use because of the fact that Oken (1835) accepted the emended form suggested by Eschscholtz, must be rejected, while *Melicertum* Eschscholtz becomes a legitimate name.

Melicerta was used by Oken (1815) to designate generically a species previously named *Medusa campanula* by Fabricius in his "Fauna Groenlandica" (1780). Eschscholtz (1829) included in his *Melicertum,* besides this species, *M. campanulatum* (Chamisso and Eysenhardt), *M. penicillatum* Eschsch., and *M. pusillum* (Swartz). Which of these four species should be selected as the type of the genus? *M. pusillum* is so poorly described that it should be assigned to "*Species incertae sedis.*" *M. penicillatum* can be reasonably well identified, but it has been made the type of another genus, *Polyorchis. M. campanulatum* may also be a member of *Polyorchis,* although this identification is rather questionable, and hence its choice is not recommendable. Thus our choice must fall on the sole remaining species, *M. campanula,* i.e., on Oken's type for *Melicerta,* and evidently intended as a type by Eschscholtz.

The answer to our question thus is that the name *Polyorchis* as used by A. and L. Agassiz is justified.

(This decision, however, does not imply that these investigators were right in their usage of the name *Melicertum.* Indeed, the chances are that they were wrong in this respect. Whether Mayer's [1910, p. 207] solution to this problem is acceptable may well be questionable. It may, perhaps, be advisable to have this nomenclatorial tangle settled by the International Commission on Zoological Nomenclature since, if a review is carried out in strict accordance with rules, it will imply a number of rather unfortunate changes.)

Subgenus **Polyorchis**

Diagnosis: Gastric peduncle of moderate size, as shown by the fact that point of origin of manubrium is never more than 0.40 the height of bell from exumbrellar apex. Manubrium long or of moderate length, always longer than gastric peduncle. An ocellus on base of every tentacle.

Type Species: *Polyorchis penicillatus* (Eschscholtz).

Remarks: To decide how many of the recorded forms should be referred, as species, to this subgenus is fraught with difficulties because of two conditions: first, the subgeneric delimination must still be regarded as tentative; second, the fact that very similar species may occur within a very narrow distributional range, as exemplified by *P. penicillatus* and *P. montereyensis* (within 80 English miles of each other), and the fact that many of the previous investigators have submitted their material to comparatively superficial inspection, force us to proceed with the greatest caution when the question arises whether forms previously recorded and identified really are specifically identical.

Here follows an enumeration of the forms of this group which have been named up till the present time: *Polyorchis penicillatus* (also named *Melicertum penicillatum* Eschscholtz; *Aglaura penicillata* Blainville; *Polyorchis eschscholtzii* Haeckel); *P. campanulata* (also named *Medusa campanulata* de Chamisso and Eysenhardt; *Melicertum campanulatum* Eschscholtz; *Melicerta campanulata* Blainville; *Polyorchidium campanulatum* Haeckel; *Campanella chamissonis* Lesson); *Polyorchis pinnatus* Haeckel; *P. minuta* Murbach and Shearer; and *P. karafutoensis* Kishinouye. What is the systematic status of these several forms? In regard to *P. penicillatus,* see the following discussion under the treatment of this form.

Mayer (1910, p. 218) suggested that *Medusa campanulata* Chamisso and Eysenhardt, 1821, may be a synonym of *Polyorchis penicillatus*, indicating his doubt, however, by adding a question mark. If we are to accept at all the data in the original description, this identification must be unhesitatingly rejected, even though we take into account the evident incompetence with which the description was made. The most revealing difference is to be found in the arrangement of the tentacles. In *Medusa campanulata*, as in *Polyorchis (Scrippsia) pacifica*, the oldest tentacles are quite far removed from the umbrellar margin; while in *Polyorchis penicillatus*, their removal from the margin is very slight. Considering the emphasis placed on this feature in Plate 30, Figure 1*a*, of Chamisso and Eysenhardt (1821) and its systematic significance in this group of medusae (of which these authors knew nothing!), it can hardly be considered as justifiable to neglect it or to discard it as due to erroneous observation and recording. Most other authors have accepted this form as a distinct species. It may even be subgenerically different (see above, p. 108).

Polyorchis pinnatus Haeckel (1879, p. 149) was identified with *P. peni-*

cillatus by Mayer (1910, p. 218). Had Haeckel's single specimen of this form been taken in San Francisco Bay, this decision would undoubtedly have been fully justified. However, its locality was Honolulu in the Hawaiian Islands; i.e., it came from a region that shows little faunistic relationship to the California waters. This, of course, makes it necessary to proceed with caution.

Haeckel's specimen of *P. pinnatus* measured about 30 mm. in height, according to the magnification given for his Plate 8, fig. 13. The following specific features were particularly noted: (1) Radial canals, proximally to peduncular bend, without branches; distally to this bend, with 12–15 pairs of branches. (2) Tentacles, of uniform length, 40 in number. (3) Each radial canal with 8 gonads. From this it is evident that *P. pinnatus* agrees with the San Francisco Bay form of this genus in regard to the number of gonads while at the same time it differs very decidedly in respect to the number of tentacles: a specimen of *P. penicillatus* only 19 mm. high has not less than about 100 of them as compared with 40 in a specimen of *P. pinnatus* of 30 mm. height. The number of side branches on the radial canals also exhibits distinct differences. Other differences also may be adduced, e.g., the lengths of the tentacles and the arrangement of the branches on the radial canals. Unfortunately, however, it is probably fair to assume that these are in part due to Haeckel's somewhat superficial treatment of his material. Even so, the differences are too large to allow us to establish identity, at least until further observation on Hawaiian material justifies such procedure, especially if we also take the difference in geographical locations into consideration, as well as the systematic differentiations this genus exhibits along the California coast.

It may finally be noted in this connection that *P. pinnatus* does not agree sufficiently with any of the other forms of this genus occurring on the west coast of North America to justify full systematic identification; and that therefore, for the time being at least, it must be regarded as a distinct species.

There can be no doubt that *Polyorchis karafutoensis* is a distinct species; see Uchida (1925, p. 88, Fig. 13).

While the systematic positions of these forms may be regarded as reasonably certain, the nature of those forms of *Polyorchis* on the west coast of North America which are furnished with branched radial canals is very difficult, if not impossible, to decide at present with anything approaching scientific certainty, due to the absence of sufficient data. We can state with certainty that we have forms which show quite characteristic differences, while at the same time they present so striking similarities that unity of species at first sight appears probable. It may be that the observed differences are caused by direct environmental modifications and that they are not inherited, but until this has been proved experimentally, there seems to be no choice except to assume tentatively that we are concerned with systematically distinct forms which, in the absence of clear-cut transitions, probably should be best regarded as species.

The only form of this kind, besides *Polyorchis penicillatus*—the type species of the genus—named up till the present time, is *P. minutus*, a species established by Murbach and Shearer (1903, p. 174) on a single, small specimen taken in Puget Sound, Washington. The authors stressed that what they called Fewkes's "revised version" of *P. penicillatus* approached their new species "very closely. In fact we have only ventured to give it separate specinc rank on account of size, a feature of no very great importance." They had found that their specimen, measuring only 15 mm. in height, was sexually mature, judged by the long gonads, and this size appeared to them too small to be compatible with previously published data.

There can be no doubt that *P. minutus* is very closely related to *P. penicillatus;* indeed, it would be rash to separate these two specifically if we had available only the descriptive and pictorial material given by Murbach and Shearer (1903). Fortunately, this is not the case. Foerster (1923, pp. 222, 226, 228, 232, and 250) presented under the name of *P. penicillata* observational data on a large material from Puget Sound. Judging by these data as well as by observations made by me on specimens from this locality, collected by Dr. T. Kincaid, I have concluded that we are concerned with a special form, different from the California species, and hence that the name of *P. minutus* should be maintained as a specific denotation. A very striking difference is found, for example, in the coloration. Foerster (*loc. cit.*, p. 251) states that *P. minutus* has the gonads, manubrium, and tentacle bulbs of a purple color, a condition found neither in *P. penicillatus* nor in *P. montereyensis*. Because the specimens which I obtained from Puget Sound were all large (more than 30 mm. high) and hence could not yield sufficient data for a detailed description, I have decided to desist from attempting to write a supplementary description and simply refer to Murbach and Shearer (1903) and to Foerster (1923, p. 250). It may finally be noted that Mayer, in his large "Medusae of the World," 1910, p. 219, states that the ocelli in *P. minutus* (which he accepts as a valid species) are yellow. This is misleading, yellow being the color only in preserved specimens. (Besides, by Murbach and Shearer, 1903, p. 174, *P. minutus* was noted by these authors in 1902, pp. 71, 72; Maas, 1904, pp. 425, 442; Mayer, 1910, p. 219; and Foerster, 1923, pp. 250, 251, who also noted this form under the name of *P. penicillata* on pp. 222, 226, 228, 232).

In regard to *P. penicillata* recorded by Fewkes (1889*a*, *b*) as well as the specimen recorded under this name by Bigelow (1940), see pages 120, 121, under "Remarks" to *P. penicillatus*.

Murbach and Shearer (1903, pp. 175–76) were right when they criticized Haeckel's (1879, p. 149) inclusion of the paired arrangement of some pinnate branches of the radial canals in the generic diagnosis of *Polyorchis*. This arrangement of the branches in the earliest published figures (Eschscholtz, etc.) is undoubtedly, as they suggested, simply due to the crudeness of the representation. Likewise, they were probably right when they criticized

Fewkes (1889*a, b*) for his representation of all these branches as paired in what he terms *Polyorchis penicillata* from southern California.

In addition to the forms of *Polyorchis* accepted in the foregoing as distinct species, I introduce in this report two new species, both from Monterey Bay, California, viz., *P. montereyensis*, with branched radial canals, and *P. haplus,* with simple radial canals. Since this study was begun on *P. montereyensis,* and since I have had available a much larger and more varied material of this form than of *P. penicillatus,* I have chosen to present it first and to give to it an elaborate description to be used for the purpose of comparison.

Polyorchis (Polyorchis) montereyensis Skogsberg, new species

Description: The largest among the hundreds of specimens seen by me were about 40 mm. high. Umbrellar outline somewhat variable; presents no distinct progressive change with age. Ratio between height and greatest width of body, 1.2 (1.0–1.6) : 1. Greatest width either about the middle of bell or near level of attachment of gonads. Aboral end of exumbrella usually almost semicircular in lateral outline and varies from this type gradually to the extremes of broadly conical shapes represented by Agassiz (1865, Fig. 179) and by Fewkes (1889*a,* Pl. 23); all of these shapes were found mingled with each other in Monterey Bay. Lateral sides of umbrella either broadly convex, with bell opening constricted (ratio between greatest width of bell and width of bell opening, about 1.3–1.4 : 1); or sides are more or less flattened, especially orally, the noted ratio sometimes being as low as 1.1 : 1. Velar opening about 0.6–0.7 the umbrellar opening (about as in Pl. 23 of Fewkes, 1889*a*); I never found it as small as indicated by Little (1914, p. 310, Pl. 13). Mesoglea quite firm, enough so to maintain shape of medusa out of water except for closing of umbrellar opening. Point of origin of manubrium about 0.25–0.40 the height of bell from exumbrellar apex (which shows size of the rounded gastric peduncle); it should be noted that my smallest specimen was about 6.0 mm. high; in still smaller specimens, this peduncle probably is smaller, as indicated by Fewkes (1889*b*, p. 106) and Foerster (1923, p. 252).

Tentacles increase in number throughout life; arranged in 1–4 fairly distinct, concentric circles, the number of circles depending on age of specimen; in specimens of the usual sizes (15–25 mm. high), number of circles is 3. Number of tentacles varies as follows in relation to height of bell: (height of bell, 1–4 mm., tenacles, first 4 and then 8; these values are assumptions since I have not as yet seen any specimens of these sizes); height of bell 5 mm., tentacles 16; bell 6–10 mm., tentacles 24; bell 8–10 mm., tentacles 32; bell 10–15 mm., tentacles 40; bell 12–17 mm., tentacles 44; bell 17–20 mm., tentacles 48; bell 25–30 mm., tentacles about 72; bell about 35 mm., tentacles around 80. From this it will be seen that there is a considerable variation in regard to the ratio between the size of the bell and the number of tentacles.

Even more striking deviations from the typical ratios were observed. Thus, in a couple of specimens about 18 mm. high, the number of tentacles was not less than 64; and in one of 26 mm., I counted as many as 88. All of these variations were found in one and the same population, taken within the harbor of Monterey. What the maximum number is is not known. In old specimens, size differences among earlier tenacles become negligible, if not obliterated. Oldest tenacles are hardly at all removed from the bell margin. When relaxed, medium-sized specimens may have tentacles as much as five times longer than bell is high. Tentacular bulbs, if present, are not marked off clearly from rest of tentacles.

In specimens about 6.0 mm. high, manubrium extends, when relaxed, to a point about ⅔ the height of bell from apex of exumbrella; in specimens about 7.0 mm. high, it may extend to velum; and in older specimens it may extend slightly beyond this structure. In specimens as large as 10 mm., oral lips may be nearly even, but usually marginal folding begins somewhat earlier than in this stage.

In specimens about 6.0 mm. high, each radial canal may have as few as 10–12 knob-like side branches on either side, beyond peduncular bend; but this number may be as high as 20–25 at this early stage, i.e., within the range characteristic of older specimens which is from 19 to 33. Thus the full number of these branches seems to develop nearly simultaneously at a very early stage. Sometimes almost the entire range of variation has been found in the 4 canals of a single specimen; the prevailing numbers are 25–30. Most of the branches of the two sides of each canal alternate irregularly; see "Remarks" to subgeneric diagnosis, page 112; proportion of paired branches varies even among the 4 canals of each specimen. From their knob-like beginning, most of the branches increase in length, some, although seldom, reaching a maximum length of about 0.20 the distance between radial canals. Longest branches occur near the middle of bell; in oral portion of radial canals, branches usually more or less small and rather few in number. Scattered among the longer branches there are often a few smaller ones (some of which may possibly be of later development); among these there may be some which are so small that it is difficult to decide whether they should be counted, a fact that makes the establishment of the number of branches uncertain. At first, side branches are simple, fairly straight, and nearly at right angles to radial canals. Later a variable number of them begin to become irregularly bent, slightly enlarged distally; or they send out, in distal half, 1–4 short, irregular secondary branches. In exceptional cases, a few of these secondary branches may even anastomose with neighboring branches of the same radial canal, thus forming local reticulation. In regard to these irregularities, it should be especially noticed that the 4 radial canals may be quite independent in their variations. In this connection it should be added that, although very rarely, even the main radial canals may be more or less irregular; thus I have seen specimens in which 1 or 2 of these canals had a more or less zigzag course. At place where radial canal bends over on gastric peduncle ("peduncular bend"), there are, on either side of canal, about 7–10 closely-set, fine, somewhat irregular but not much branched branches, the longest of them usually somewhat shorter than longest branches beyond this bend. On radial canals of gastric peduncle, thus among gonads, branching is very variable. Often 1–2 of these canals are unbranched or furnished with only a few short branches; at other times, there are 5–8 medium-sized branches on either side of each canal; and in one specimen, 25 mm. high, I even found these branches of the 4 radial canals quite well anastomosed. In each quadrant, ring canal usually has about 8–15 irregularly spaced, blind branches, most of them very short, knob-like; sometimes their length may be as much as five times width of ring canal (Agassiz, 1865, Fig. 183); they may even show signs of branching. As many as 16–20 were counted in the quadrants of one specimen, and in all probability larger numbers will be found; exceptionally, specimens were found with no branches of this kind. There was no regular spacing between these branches and canals leading to tentacles.

When comparatively few, gonads usually are located near middle of radial canals on gastric peduncle; when many, they occupy nearly entire length of these peduncular canals. Number of gonads difficult to establish for two reasons: first, some gonads may be so small that it is nearly arbitrary whether they should be counted; second, some gonads are branched in many specimens. Branching may take place at any level of gonad; when it occurs very close to radial canal, it may become almost impossible to decide with certainty whether there is a common part or whether "branches" originate directly from radial canal. Gonads begin to appear in specimens 5–6 mm. high and increase in number with age. Mature gonads may be found in specimens about 13 mm. high. Number of gonads on each radial canal varies even among the 4 canals of each specimen; thus, for example, in a specimen 30 mm. high, these canals carried 25–29–30–34 of them. Maximum number not known; as many as 45 have been counted. Under adverse conditions, gonads are reduced; in specimens about 25 mm. high which had been submitted to prolonged starvation, as few as 6–10 were found on each canal. When fully developed, longest gonads may extend nearly to velum, while others at the same time are still very short; relative position of gonads of different lengths variable. When branched, each gonad usually has only one branch, but 2–4 branches have been recorded. Usually only a rather small number of the gonads are branched.

Basal part of each tentacle has dark red to purple coloration, often with brownish admixture. Since this tentacular part is furnished with a rounded mammilliform extension (Fig. 2) covering exumbrellar side of bell margin, and since sizes of tentacles differ in a more or less regular sequence, this coloration assumes quite a striking and distinctive pattern. Colored zone extends often around base and covers a distance from tip of base that is slightly less to somewhat more than basal width of tentacle. Within the mammilliform projection of tentacle base the eye forms a round, red-black spot. Rest of body fairly transparent, of greyish tone, sometimes with a faint somewhat pinkish tinge. However, canals of digestive tract and of gonads tend to absorb color of food. (Thus, for instance, these structures became brown in my cultures after a richly red-brown copepod, *Tigriopus fulvus,* had been used as food. This coloration of the endodermal cells remained during quite a long period of starvation, a fact that made the study of the canal system very easy.)

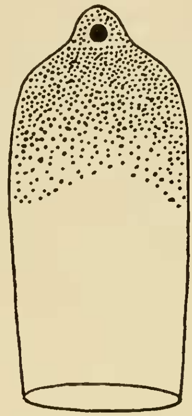

Fig. 2.—*Polyorchis montereyensis.* Diagram of base of tentacle, in which general distribution of pigmentation is indicated by stippling. In proximal portion of pigmented area, chromatophores are so close that pigment appears continuous; toward distal portion, chromatophores are more or less spaced.

Occurrence: By far the most commonly observed Hydromedusa in Monterey Bay, California, where it has been recorded throughout several years (1937–1942), from February to December, inclusive, in Monterey Harbor (type locality). In this locality the species was characterized by as yet unexplained prolonged periods of absence, followed by periods when it occurred in moderate to large numbers. Spawning specimens and specimens of very different sizes were present throughout the noted months. Hydroid stage not yet found.

Surface temperatures throughout the years 1919 to 1928, inclusive, ranged from 14.9° to 9.2° C.; the usual range is 11°–13° C. Salinity for the same period ranged from 32.5 percent to 34.1 percent, according to records taken at Hopkins Marine Station of Stanford University, located less than one English mile from the type locality (Bigelow and Leslie, 1930, Bull. Mus. Comp. Zool. Harvard Coll., 70: 5; 1930).

The species does not appear to have been recorded in literature before.

Remarks: This species differs from *Polyorchis penicillatus* of San Francisco Bay mainly in having a larger number of gonads and branches on the radial canals and a smaller number of tentacles; the pigmentation at the base of the tentacles also shows a striking and readily recognizable difference.

Polyorchis penicillatus (Eschscholtz)

Non Medusa campanulata, Chamisso and Eysenhardt, (1821), p. 359, pl. 30: 1*a*, *b*, *c*. (This, of course, also eliminates the several synonyms of this species.)

Melicertum penicillatum, Eschscholtz (1829), p. 106, pl. 8:4; Blainville, (1834), pl. 38;—Dujardin (1840), p. 160;—Agassiz, L. (1862), pp. 348, 349;—Agassiz, A. (1865), p. 119;—Haeckel (1879), pp. 136, 149, 150;—Murbach and Shearer (1903), p. 176;—Maas (1904), pp. 425, 442;—Bedot (1905), p. 144;—Foerster (1923), p. 250.

Melicertum penicillata, Lesson (1843), p. 293;—Agassiz, A. (1865), p. 119.

Aglaura pencillata, Blainville (1834), p. 283, pl. 33: 4;—Agassiz, L., (1862), pp. 348, 349;—Agassiz, A. (1865), p. 119;—Haeckel (1879), p. 150.

Polyorchis penicillata, Agassiz, A., *in* Agassiz, L. (1862), *part.*, p. 349;—Agassiz, A. (1865), *part.*, p. 119, figs. 179–183;—Haeckel (1879), *part.*, p. 150;—Murbach and Shearer (1903), *part.*, p. 175;—Bancroft (1904), pp. 43–46, 4 text figs.;—Maas (1904), pp. 425, 442;—Bedot (1905), *part.*, p. 144;—Torrey (1909), p. 16;—Mayer (1910), *part.*, p. 218, fig. 111;—Little (1914), pp. 307–328, pls. 13–15;—Johnson and Snook (1935), *part.*, p. 66, fig. 55.

Non Polyorchis penicillata, Foerster (1923), pp. 222, 226, 228, 232, 250; refers to *P. minutus*.

Polyorchis penicillatus, Haeckel (1879), *part.*, p. 149;—Maas (1904), *part.*, pp. 425, 442; —Foerster (1923), *part.*, p. 250.

Polyorchis eschscholtzii, Haeckel (1877), *part.*, no. 147; (1879), *part.*, p. 150.

Non Polyorchis pinnatus, Haeckel (1879), p. 149, pl. 8:13;—Maas, (1904), pp. 425, 442;—Mayer (1910), p. 218;—Foerster (1923), p. 250.

Polyorchis, Loeb (1906*a*), pp. 87, 88, 89, 90, 91, 141; (1906*b*), p. 427;—Maccallum (1907), p. 385.

Description: Largest specimens recorded so far, about 25 mm. high. Ratio between height and greatest width of bell, about 1.0–1.3 : 1. Greatest width either at about the middle or somewhat closer to apex of bell. Aboral end of exumbrella usually almost semicircular in lateral outline; only very few specimens have a tendency toward the formation of a small, broadly rounded apical cone. Sides of bell usually subvertical; more or less flattened, especially orally; and oral constriction frequently very slight or not developed at all. Velar opening about 0.4–0.5 the umbrellar opening (whether it ever is so small as figured by Little, 1914, Pl. 13, Fig. 1, seems uncertain). In large specimens gastric peduncle of about the same size as in *P. montereyensis*.

Tentacles increase in number throughout life; arranged in 1–4 concentric circles. Number of tentacles increases very rapidly with age, as shown by the following values: height of bell about 2 mm., number of tentacles 12–16; height of bell about 3.5 mm., number of tentacles about 24; height of bell about 10 mm., number of tentacles about 50; height of bell about 19 mm., number of tentacles about 100; height of bell about 21 mm., number of tentacles about 120. Maximum number of tentacles so far recorded, 160. In older specimens, size differences among most tentacles, except the latest ones, are nearly negligible. Oldest tentacles are but slightly removed from bell margin. In Little (1914, Pl. 14, Fig. 3), tentacles drawn in a manner suggestive of presence of large, well-marked tentacular bulbs; tentacular bulbs, if at all present, usually are not clearly marked off from the rest of tentacles. Manubrium as in *P. montereyensis*. (It may be noted that Little's [1914, p. 310] statement that there is an "enlarged sac-like stomach" at place where radial canals meet is incorrect. In accordance with family diagnosis given above, no such differentiation occurs.)

Number of branches on either side of each radial canal, beyond peduncular bend, about 16–25 of sizes about as in Little's (1914) Plate 13, Figure 1, except that among the well-developed branches shown in this figure, there are a number of scattered, very short, more or less knob-like ones. Sometimes most of the well-developed ones are about equal in size, as in the noted figure; but at other times those near the middle of bell are slightly longer than the others. Branches near margin of bell are both few and short. A varying number of the branches have 1–4 secondary branches, mostly knob-like, a few of which may in their turn be branched. In a few instances, anastomosis has been observed between neighboring branches. Proximally to peduncular bend, there are about 5–7 branches on either side of canal, of lengths about as those beyond this bend. Among gonads, there are on either side of radial canals 0–5 usually knob-like, irregularly placed branches. The 4 radial canals of each specimen vary independently of each other in respect to branching. In each quadrant, ring canal has about 0–6 irregularly spaced, blind branches, mostly knob-like, at most a few times longer than canal is wide.

Gonads located near middle of radial canals of gastric peduncle; their number small, each group containing only 4–11, averaging about 8; branching occurs, but rarely. Relative position of gonads of different lengths varies.

Pigmentation restricted to the bases of the tentacles where it is much less developed than in *P. penicillatus*. In regard to the distribution of the pigment, I refer to Little (1914, Pl. 15, Fig. 8). As will be seen from this picture, the pigment is very scarce, sometimes nearly absent outside the ocellus, occupying somewhat different patterns in different individuals. These patterns agree closely with what I have observed in freshly killed material sent me from San Francisco Bay by Dr. R. Stohler, of the University of California, Berkeley. In regard to the nature of the pigment, Little (*loc. cit.*, p. 312) gives red and brown, while Dr. Stohler informed me by letter that he had found it maroon with a purplish hue or purplish with a brownish hue—in other words, about the same colors that I found in the case of *P. montereyensis*.

Occurrence: This species is common in San Francisco Bay, California, where Little (1914, p. 308) found it from December to the middle of April. For a period of one year, beginning in the middle of December 1942, daily records of this species were made from a pier in this bay (at Berkeley) through the arrangement of Dr. R. Stohler. General estimates of frequency and size were recorded, and data pertaining to tidal phase and general weather conditions at the hour of the day when the observations were made were also entered in the records. An analysis of these data shows that *Polyorchis penicillatus* was observed near the surface all the year around, with the exception of a period from August 9 to October 8, 1943, when the records were consistently negative. During the rest of the time, no distinct regularity was evident in the occurrence. Usually at least a few specimens were seen, but there were irregular periods of absence, in some cases as long as 14 days. The causes for these periods of absence could not be deduced from the available data. The occurrence at the surface appears to be remarkably independent of the tidal phases, of rain and sunshine, and of calm and rough water; also, observations were made at various hours of the day and from these observations there appeared no indications of a daily rhythm. Finally, it may be noted that large and small specimens were seen throughout the year, although on this point the records are too incomplete for certainty of statement. No other locality for this species is as yet known.

Remarks: This species was possibly first described by Eschscholtz (1829, p. 106, Pl. 8, Fig. 4) under the name of *Melicertum penicillatum*. The original description is very incomplete and is in addition, at least in some respects, incorrect. As for the type locality, Eschscholtz simply records: "Coast of California."

Considering the fact that we evidently have more than one form of the genus *Polyorchis* along this coast, the uncertainty both in regard to description and type locality is extremely unfortunate. Indeed, perhaps it would even justify the relegation of this species of Eschscholtz to "*Species incertae sedis.*" I know of no account of the localities visited by Eschscholtz during the six years of voyages when he made his observations and collections. However, considering the fact that in the earliest part of the nineteenth century shipping in California was quite undeveloped except in the region about San Francisco, it is not unreasonable to assume that Eschscholtz secured his type material of this species while at anchor in San Francisco Bay, especially since there is a form of this general appearance which is rather common in this neighborhood. For this reason and because A. Agassiz acquired most of his material of *Polyorchis penicillata* (Eschscholtz) from San Francisco Bay, I have decided that it is reasonable to maintain this species of Eschscholtz as identifiable. A factor that contributes to the advisability of this decision is that its acceptance will imply a minimum of nomenclatural changes. Other factors worthy of notice in this connection are that Agassiz's redescription is quite acceptable, and that the form treated by him should be regarded as the type of the genus *Polyorchis*. Because of the fact that some of Agassiz' material was taken in the waters of the Strait of Georgia, British Columbia, hence in the region of *P. minutus*, *P. penicillata* Agassiz is stated as only partly identical with *Melicertum penicillatum* Eschscholtz in the list of synonyms given in the foregoing discussion.

In regard to *Polyorchis penicillata* Fewkes (1889*a*, p. 593, Pl. 23, Text Fig. 4; 1889*b*, p. 103, Pl. 4, Figs. 6, 7), it has not been included in the above list of synonyms because of its uncertain status. It was taken south of Point

Conception in southern California, and at this place there is a very decided faunistic change associated with oceanic circulatory phenomena.

Polyorchis penicillata, Johnson and Snook (1935), is furnished with a *part.* because of the color notation: "stomach, gonads, tentacle-bulbs, and radial canals are reddish brown to purple." This indicates that at least part of their material had a northern origin.

Polyorchis penicillata, Bigelow (1940, p. 296), refers to a single specimen. This is entirely too scantily described for full certainty of specific identification and, in addition, it was taken very far to the south of the type locality of this species, viz., in the Gulf of California, a region characterized by tropical waters. Considering the difficulties inherent in the classification of the species of *Polyorchis,* it was judged advisable under these circumstances not to include this record in the above list of synonyms.

In regard to the remaining names in this list, it should be noted that all of them refer either to Eschscholtz's original material or to the species described by A. Agassiz. The names referring to the latter are furnished with a *part.* to indicate the restriction attached to Agassiz' form.

The description given above is based in part on data taken from Little (1914), partly on specimens from San Francisco Bay where they had been collected by Dr. R. Stohler and kindly sent to me.

Polyorchis (Polyorchis) haplus Skogsberg, new species

Description: Largest specimens recorded were about 20 mm. high; most specimens seen were about 15 mm. high or less. Ratio between height and greatest width of body, 1.1–1.3 : 1. Greatest width either at about middle of body or somewhat above. Aboral end of exumbrella almost semicircular in lateral outline; broadly conical shapes, such as figured for *P. penicillatus* by Agassiz (1865, Fig. 179) and Fewkes (1889*a*, Pl. 23), were never seen. Lateral sides of umbrella broadly convex, usually somewhat flattened toward oral end; ratio between greatest width of body and width of bell opening, about 1.3–1.4 : 1. Velar opening, mesogloea, and point of origin of manubrium about as in *P. penicillatus.*

Tentacles arranged in fairly distinct concentric circles. Number of tentacles comparatively small. Whether there is an increase throughout life is uncertain; it should be noted that in the oldest specimen observed there were not even the slightest indications of tentacular buds despite the fact that the latest tentacles were large and well developed. Number of tentacles varies about as follows in relation to height of bell: height of bell ?–7 mm., tentacles 16; bell 8–11 mm., tentacles 18–20; bell 12–20 mm., tentacles 24 (possibly the maximum number). There undoubtedly is a greater variation in regard to ratio between size of bell and number of tentacles. Oldest tentacles hardly at all removed from bell margin. Length of manubrium about as in *P. penicillatus* but in large specimens lips appear to be slightly less folded than in that species.

In specimens up to about 17 mm. high., all canals appear to be simple, i.e., without any side branches. In the oldest specimens (about 20 mm. high), the radial canals are either simple or are furnished with closely set, knob-like branches, less than or about as long as width of canals; ring canal may also be furnished with a few branches of this kind, and, occasionally, both types of canals may be furnished with a few somewhat longer, simple branches at about right angles to main canals. Thus in most specimens of this species as yet recorded, all canals were simple, and it is to this peculiarity that the species owes its name. Bend of radial canal at base of gastric peduncle forms, on the average, a more pronounced and acute angle than in *P. penicillatus;* and this feature emphasizes the fact that the peduncle is more conical than in the noted species.

When comparatively few, as in young specimens, gonads are located on inner half of radial canals of gastric peduncle; when many, they occupy entire length of peduncular canals. Number of gonads is difficult to establish for same reasons as in *P. penicillatus;* number appears to vary between 20 and 25 on each canal in fully developed specimens. When fully developed, longest gonads reach nearly to velum. Those close to manubrium usually are the longest, and this causes gonads to appear to be more crowded to manubrium than in *P. penicillatus.* Only a small number of gonads are branched; I have not seen more than one branch to any gonad. Mature gonads may be found in specimens about 12–13 mm. high.

There is a small area of deep red pigment around each eye, not much larger than the mammiliform projection on which the eye is placed. Tentacles and gonads of a yellowish tinge, sometimes quite canary yellow; this color, which is quite characteristic of the species in contrast with *P. penicillatus,* remains even after a prolonged period of starvation in aquarium. In some specimens, however, the yellow is very faint, yielding to a greyish-brown tinge. Rest of body fairly transparent and of a greyish tone.

Occurrence: So far recorded only at Monterey (type locality), where it was found in the harbor as well as in shallow water off a sandy beach; in latter place it was taken while dredging for sand dollars (*Dendraster*). Rare or moderately common from August to November.

Remarks: The presence of a species with unbranched radial canals within the genus *Polyorchis* is very interesting indeed, since it clearly indicates that the branching phenomenon does not have the fundamental significance attributed to it by many of the leading taxonomists of the Hydromedusae. As a matter of fact, the branching of the radial canals offers many excellent examples of the important role played by convergence in the evolutionary history of this group. It may be of interest to recall in this connection that Murbach and Shearer (1903, p. 177) state that the comparatively late appearance of the branches on the radial canals, in the postembryonic development, "points to their being a recent acquisition in the evolution of the race, probably within the limits of this particular group" (*Polyorchis*).

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